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Title: Experimental traffic noise attracts birds during the breeding season

Short title: Traffic noise attracts breeding birds

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Abstract: Understanding how anthropogenic disturbance affects animal behavior is challenging because observational studies often involve co-occurring disturbances (e.g., noise, lighting, and roadways), and laboratory experiments often lack ecological validity. During the 2016 and 2017 avian breeding seasons, we investigated the effects of anthropogenic noise and light on the singing and spatial behavior of wild birds by independently manipulating the presence of each type of disturbance at 89 sites in an otherwise undisturbed boreal forest in Labrador, Canada. Each treatment was surrounded by an 8-channel microphone array that recorded and localized avian vocalizations throughout the manipulation. We analyzed the effects of noise and light on the timing of the first vocalizations of each species at each array during the dawn chorus, and on the proximity of the vocalizing birds to the disturbance when those songs were produced. We analyzed all species combined, and then conducted separate analyses for the six most common species: boreal chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, white-throated sparrow, and yellow-rumped warbler. When all species were analyzed together, we found that traffic noise attracted vocalizing birds. There was some evidence that light repelled birds, but this evidence was inconsistent. In our species-specific analyses, yellow-rumped warbler sang earlier in response to noise; Swainson's thrush was attracted to noise and the combination of noise and light, but repelled by light alone. Our study provides some of the first experimental evidence of the independent and combined effects of traffic noise and light on the vocal and spatial behavior of wild birds, and suggests that breeding birds may be attracted to noisy roads where they could be

exposed to additional forms of disturbance.

Key words: anthropogenic light; anthropogenic noise; bird; birdsong; light pollution; microphone array; noise pollution; passerine; spatial ecology

INTRODUCTION

Urban and industrial developments produce multiple anthropogenic disturbances that negatively impact wildlife (McKinney 2008). Some, such as chemical contamination and anthropogenic structures, can kill animals quickly and directly (Harrison et al. 1997; Bernardino et al. 2018), but others have more subtle and prolonged effects that can be difficult to detect. In the last century, anthropogenic noise and light from cities, roadways, and industry have been recognized as widespread forms of disturbance that affect the physiology, ecology, and behavior of animals (Longcore and Rich 2004; Shannon et al. 2016). Although all animals are at risk, birds may be especially vulnerable because they frequent noisy and illuminated areas and rely heavily on acoustic communication (Longcore and Rich 2004; Slabbekoorn and Ripmeester 2008; Ortega 2012).

Birds exposed to anthropogenic noise can experience several adverse effects. They can incur physical damage, including brain deformities, hearing loss, and deafness (Marler et al. 1973), cognitive impairments, including learning and memory deficits (Potvin et al. 2016), and physiological stress, including rapid heart rate and elevated stress hormones (Kleist et al. 2018). Noise can also alter a bird's behavioral ecology by interfering with acoustic communication (Ortega 2012). For example, noise can interfere with predator avoidance by masking predator cues and conspecific alarm calls (Templeton et al. 2016), and with reproductive behavior by masking or altering sexually selected acoustic displays (Halfwerk et al. 2011a). The effects of noise on song are especially well-documented, with several studies showing that high-energy, low-frequency noise, such as traffic noise,

causes birds to shift the timing of song production and to alter the structure of individual songs in ways that are thought to minimize masking (Ortega 2012; Dominoni et al. 2016). For example, birds living in noisy environments can shift song production to quieter parts of the day and increase the amplitude, minimum frequency, tonality, and duration of their songs (Hanna et al. 2011; Ortega 2012). In some cases, birds might avoid noisy, but otherwise ideal, habitats in favor of habitats that are suboptimal in other respects (Bayne et al. 2008). It is also possible that birds may not be able to avoid noise because of its pervasiveness in most ecosystems, including in protected areas (Mennitt et al. 2014).

Like noise, anthropogenic light has adverse effects on birds (Longcore and Rich 2004). It can impact sleep and circadian rhythms, which can alter the timing of critical activities (Longcore and Rich 2004; Dominoni et al. 2013; Da Silva et al. 2015). For example, artificial lighting causes birds to initiate reproduction prematurely (Kempenaers et al. 2010; Russ et al. 2017). Light can also affect the spatial ecology of birds. For example, seabirds and migrating songbirds approach artificial lighting, which can increase their risk of predation and collision (Longcore and Rich 2004; Montevecchi 2006; van Doren et al. 2017), and European blackbirds (*Turdus merula*) preferentially select artificially illuminated nest sites (Russ et al. 2017).

Understanding the effects of anthropogenic noise and light on birds is challenging because noise, light, and the structures that produce them (e.g., cities, roadways, and industry) often co-occur. Some studies compare disturbed populations living near cities, airports, or highways to populations in areas of minimal disturbance (Dominoni et al.

86 2013). However, cities, highways, and airports combine habitat alteration, pollution, and
87 altered biological community compositions, which has made ascertaining the independent
88 effects of noise and light, or any other specific form of disturbance, difficult (Summers et
89 al. 2011; Nenninger and Koper 2018). Laboratory experiments on captive animals can
90 disentangle the effects, but often omit important ecological factors and may not translate
91 to the wild. Consequently, there is a need for experimental manipulations on wild birds to
92 fully understand how anthropogenic noise and light affect their behavior.
93 In this study, we manipulated the presence of anthropogenic noise and light to
94 better understand their independent and combined effects on the singing and spatial
95 behavior of wild birds. We focused on the order Passeriformes because passerines are
96 primarily diurnal and thus vulnerable to the effects of nocturnal lighting. They also rely
97 heavily on vocal communication for attracting mates, repelling rivals, and coordinating
98 activities with offspring and other conspecifics (Bateson and Feenders 2010).
99 Based on previous, largely correlational, studies, we made several predictions
100 about how birds would respond to experimental noise and light. First, traffic noise should
101 cause birds to distribute their vocalizations more evenly throughout the day (Fuller et al.
102 2007; Cartwright et al. 2014) and, therefore, to be heard earlier in the morning. European
103 robins (*Erithacus rubecula*) and red-winged blackbirds (*Agelaius phoeniceus*) living in
104 noisier environments both shifted song production from the dawn chorus, which coincides
105 with peak traffic, to quieter times of the day, such as mid-day or night (Fuller et al. 2007;
106 Cartwright et al. 2014). Second, noise should repel birds. Summers et al. (2011) found that

107 species richness increased as the distance from the road increased and the amplitude of
108 the associated traffic noise decreased, suggesting that birds avoid noisy roadways. Third,
109 night lighting should attract birds, since other studies have found that seabirds and
110 migratory songbirds are attracted to artificially lit structures (Montevecchi 2006; van
111 Doren et al. 2017), and that breeding European Blackbirds preferentially select artificially
112 illuminated nest sites (Russ et al. 2017). Fourth, night lighting should cause birds to sing
113 earlier, as has been shown in several songbird species (Kempenaers et al. 2010; Da Silva et
114 al. 2015). Finally, we predicted that birds in the presence of artificial noise and light would
115 be heard even earlier than when only noise or light were present, and that the repellent
116 effects of noise would offset the attractive effects of light.
117
118 **METHODS**
119 **Study area**
120 We conducted 110 trials during the 2016 (*N* = 68) and 2017 (*N* = 42) avian breeding
121 seasons (16 May to 10 July). Trials were distributed across a 50 x 50-km area near Happy
122 Valley-Goose Bay, Labrador, Canada. This area is part of the Boreal Shield Ecozone, which
123 is a large (approximately 1.8 million km^2) and relatively undisturbed region that provides
124 substantial habitat for breeding birds. Windspeed at the study site was also known to be
125 low, which is important for detecting and recording acoustic signals. The site was
126 therefore ideal for recording avian responses to experimental noise and light in an
127 otherwise undisturbed forest. Black spruce (*Picea mariana*) and balsam fir (*Abies*

balsamea) were the dominant tree species, though tamarack (*Larix laricina*), white birch (*Betula papyrifera*), heart-shaped birch (*B. cordifolia*), and trembling aspen (*Populus tremuloides*) were also present. Within the study area, trial locations were selected at random by generating non-repeating UTM coordinates with the website random.org, plotting those points on 1:50,000 scale topographic maps (National Topographic System, Series A771, Edition 4MCE, Map13 F/7 – 13 F/10), and discarding any points that were not within 0.5–1 km of road or trail access, or which were within a swamp, water body, or 0.5 km of another trial location. We separated trials by at least 0.5 km to reduce the risk of birds being detected at multiple sites (Wilson and Mennill 2011), and we excluded locations that were beyond 1 km from road or trail access because carrying our equipment through dense forest over distances greater than 1 km would have been difficult. As part of another study (JP Ethier, unpublished data), 20 locations used in 2016 were re-used in new trials in 2017. We consider these trials as independent replicates because they involved different treatments each year and there was high species turnover at each site between years.

Microphone arrays

At each trial location, we set up an 8-channel microphone array that allowed us to record and localize avian vocalizations throughout the trial. Each array consisted of four digital audio recorders (Model: SM3; Wildlife Acoustics, Concord, MA, USA) attached to trees, approximately 1.5 m above the ground, at the four corners of a 40 x 40 m square. Each

149 recorder had two microphones: one was built into the recorder (omnidirectional pickup
150 pattern; 50–20000 Hz (± 10 dB) frequency response) and a second, external microphone
151 (model: SMM-A2; omnidirectional pickup pattern; 50–20000 Hz (± 10 dB) frequency
152 response) was positioned in the forest canopy approximately 2 m above the first.
153 Separating microphones in the vertical dimension allowed us to localize birds in three-
154 dimensional space. We elevated the external microphone with a painter's pole and fixed it
155 in place by hooking an attached wire over a tree branch. The microphones were pointed
156 towards the center of the array, and their locations determined with a survey-grade global
157 navigation satellite system (GNSS) with 10-cm accuracy (model: Trimble Geo 7X; Trimble
158 Inc., Sunnyvale, CA, USA). As a requirement for acoustic localization, the clocks of the four
159 audio recorders were synchronized to within 1 ms of each other by connecting them to
160 external GPS units (model: Garmin SM3 GPS) for the duration of the trial (Mennill et al.
161 2012).
162 Audio recorders were programmed to record continuously until manually stopped,
163 creating a new stereo audio file every 2 h (WAVE format, 24 kHz sampling rate, 16-bit
164 amplitude encoding, 220 Hz analog high-pass filter, 10 dB analog voltage gain). We had
165 four microphone arrays in 2016, and, on average, were able to set up two arrays at new
166 locations each day. In 2017, we had two microphone arrays, with one being set up each
167 day. Arrays were set up in the afternoon and recorded for a minimum of 48 h. The first 24
168 h was used as part of another study and involved no manipulations (JP Ethier, unpublished
169 data). The next 24 h served as an experimental period in which we recorded singing

behavior during and after experimental disturbance treatments were broadcast.

We set a Kestrel 5500 weather station (Kestrel Meters, Boothwyn, PA, USA) inside each array. Every 20 min, it recorded temperature (± 0.1°C), windspeed (± 0.1 km/h), relative humidity (± 0.1%), and barometric pressure (± 0.1 mb). Temperature influences the speed of sound, which is required for the sound localization process. Wind can influence the likelihood of detecting signals on recordings, but windspeed was always low (mean = 0.75 km/h, sd = 1.65 km/h), and therefore was not considered further. Humidity and barometric pressure were not considered in subsequent analyses because they have negligible effects on the speed of sound (Wölfel and McDonough 2009).

Disturbance treatments

We returned to the array before 1700 h on the day after it was set up and installed one of four disturbance treatments: (1) no light and no noise (control; *N* = 39); (2) light but no noise (*N* = 35); (3) noise but no light (*N* = 17); or (4) noise and light (*N* = 19). Treatments were selected at random, but with the constraint that the speaker used to broadcast noise could only be used every second day due to the time needed to recharge its battery. The sample sizes for treatments involving noise were thus smaller than for other treatments.

Noise was broadcast from an amplified loudspeaker (model: SBT1009BK; speaker diameter: 20.3 cm; The Sharper Image, Farmington Hills, MI, USA) placed facing upwards in the center of the array. The speaker was connected to an external lithium ion battery (model: Car Rover B019DVZXTE; 26 amp-hour; 12-V; Startwayauto Store, Guangzhou,

191 Guangdong, China) that supplemented its internal battery, and to a digital audio player
192 (model: HS-636-4GBBK MP3 Player; Hipstreet, Markham, ON, Canada) that played the
193 noise stimulus. The entire apparatus was sealed inside a black plastic bag to protect it
194 from rain. The noise stimulus was programmed to begin playing at 1700 h (ca. 24 h after
195 the array was set up) and to continue for 15 h (until 0800 h the following morning).
196 The noise treatment included three noise stimuli that were derived from online
197 sources and which, together, represented a range of traffic types. They varied primarily in
198 terms of traffic rate. The first stimulus was recorded from a country highway and was 1 h
199 in length, with approximately seven vehicles passing per minute. The second stimulus was
200 recorded from a two-lane highway, with approximately 10 vehicles passing per minute,
201 and was 8 h in length. The third noise stimulus was recorded from a busy freeway, with
202 approximately 40 vehicles passing per minute, and was 8 h in length. Using Audacity
203 software (version 2.0; Audacity® software is copyright © 1999–2018 Audacity Team; the
204 name Audacity® is a registered trademark of Dominic Mazzoni), each stimulus was
205 normalized to a peak amplitude of -1 dB and then repeated to construct a 15-h playback
206 sequence. The three traffic noise stimuli were assigned at random to trials involving noise
207 (first stimulus N = 13 trials; second stimulus N = 14 trials; third stimulus N = 9 trials).
208 During playback in the field, we set the volume on the speaker and the digital
209 audio player to 'maximum' to ensure that all stimuli played at approximately the same
210 amplitude in different trials. Using a digital sound level meter (model 33-2055; C
211 weighting; fast response; 50–126 dB range; ± 2 dB accuracy; 0.0002 micro bar reference;

212 RadioShack Corporation, Fort Worth, TX, USA), we measured the peak amplitude of the
213 stimulus over a 5-min period at six predetermined distances from the speaker at the
214 beginning of six different trials, when the speaker's battery was fully charged. Peak
215 amplitudes (mean ± SD) were 84.8 ± 2.8 dB at 1 m, 70.3 ± 9.5 dB at 5 m, 61.5 ± 8.1 dB at
216 10 m, 54.3 ± 3.9 dB at 15 m, 50.5 ± 1.2 dB at 20 m, and < 50 dB at 25 m.
217 The light treatment was a battery powered light emitting diode (LED; power: 6 W;
218 Super Bright LEDs Inc., St. Louis, MO, USA) that was hung by its power cable from a tree
219 branch at an average height of 4.3 m (SD: 0.8 m; range: 2.6–5.7 m) in the center of the
220 array. At this height, the light's 40° beam angle provided an average area of ground
221 illumination of 7.8 m^2 (SD: 2.9 m^2; range: 2.7–13.5 m^2). The light was connected to a light-
222 sensitive switch (model: GLUX-DDS Dusk-to-Dawn Sensor) that activated the light at
223 approximately sunset (78 lux, as measured with a digital light meter; accuracy: 5%; model:
224 401027; Extech Instruments, Boston, MA, USA) and deactivated it at sunrise (219 lux). At
225 the time and location of our study, the average sunset occurred at 2122 h (range:
226 2057–2133 h) and the average sunrise occurred at 0440 h (range: 0433–0459 h;
227 www.timeanddate.com, 2018). In trials involving noise and light treatments, we
228 attempted to hang the light directly above the speaker, though vegetation and
229 topography sometimes required them to be separated slightly (mean ± SD horizontal
230 distance: 2.7 ± 2.2 m). We chose LEDs, as opposed to other types of lighting, because LEDs
231 are common, energy-efficient, durable, and available in diverse colors (Mottier 2009).
232 For each trial involving light, we randomly selected one of five LED colors that are

233 used in exterior lighting and that wild birds might encounter: red (*N* = 12 trials; model:
234 GLUX-RGB18W-S40B-MCL; color: 622 nm), green (*N* = 11 trials; model GLUX-RGB18W-
235 S40B-MCL; color: 528 nm), blue (*N* = 9 trials; model GLUX-RGB18W-S40B-MCL; color: 474
236 nm), cool white (*N* = 13 trials; model GLUX-CW6W-S40; correlated color temperature:
237 5800 °K), and warm white (*N* = 9 trials; model GLUX-WW6W-S40B; correlated color
238 temperature: 3100 °K). White lights would be the most frequently encountered by
239 passerine birds, but exposure to other colors is also likely to occur. Including multiple light
240 colors ensured that our stimuli represented diverse forms of light disturbance.
241
242 **Acoustic analysis**
243 For each 2-h interval of a trial, we used Audacity software to combine the set of four
244 stereo audio files that had been recorded simultaneously by the array into a single 2-h, 8-
245 channel sound file (WAVE format; 16-bit amplitude encoding; 24 kHz sampling rate). The
246 8-channel file was named according to the array number, date, and start time of the
247 recording. Using Audacity, we viewed as spectrograms (512-point fast Fourier
248 transformation, 87.5% overlap, Hamming window) all 8-channel audio files recorded
249 between midnight and 0800 h on the night when the treatments were deployed. During
250 the data scoring process, we remained blind to the disturbance treatment. Whenever we
251 detected a vocalization from a passerine, we noted its onset and offset and annotated it
252 according to species, which we defined according to the online Checklist of North and
253 Middle American Birds (Table 1; Chesser et al. 2018). For most species, we annotated their

species-specific songs, but, for boreal chickadee, red-breasted nuthatch, and common raven, which do not produce songs, we annotated their species-specific calls (Rodewald 2015). We included vocalizations only if they were visible on the audio channels corresponding to at least three of the four corners of the array, since vocalizations can only be localized when they are detected at three or more locations in an array (Mennill et al. 2012; Wilson et al. 2014). Based on our previous experience with this array configuration, vocalizations detected by one or two recorders only originate from at least 40 m away from the center of the array (personal observation; Wilson et al. 2014). Finally, we annotated only the first 10 vocalizations produced after midnight by each species, or all of the vocalizations from a species if it produced fewer than 10.

Vocalizations were localized automatically using a custom program in MATLAB (Version 6.1, The MathWorks, Natick, MA, USA). For each vocalization, the program uses information about its position within the parent file to open the 8-channel clip containing the vocalization. The program applies a species-specific high-pass filter to remove low-frequency background noise (Table 1). It then identifies the channel with the highest signal-to-noise ratio and uses waveform cross-correlation to measure the time-of-arrival differences of the signal between that channel and the other seven channels in the array. The program then simulates a 3-dimensional lattice over the study area, and, for each vertex in the lattice, calculates how long it would take for a sound to reach each microphone in the array, as well as the corresponding time-of-arrival differences among the microphones. For each vertex, the sum of the absolute differences between the

theoretical and observed time-of-arrival differences are calculated and used as a unitless measure of localization error. Localization error is a measure of model fit, not a measure of geographic distance. The vertex that minimizes localization error is selected as the best estimate of the origin of the sound.

Vocalizations were removed from further analysis if their localization error exceeded 0.02. Previous research involving the playback of sounds from known locations within our arrays (but after our trials were complete) showed that 90% of localizations with an error value of 0.02 or less were within 3.6 m of their true locations, as determined by our GNSS (JP Ethier, unpublished data). For each remaining vocalization, we calculated the distance between its estimated origin and the experimental disturbance using the R packages 'sp' (Bivand et al. 2013) and 'rgeos' (Bivand and Rundel 2018). If both a light and speaker were present, we calculated the distance to the midpoint between them, and, if the speaker and light were both absent, we calculated the distance to the center of the array. We excluded from further analysis any vocalizations that were more than 30 m away from the disturbance, or, for control trials, from the center of the array. A 30-m radius around the disturbance ensured that vocalizations originated from locations within or close to the array. Beyond 30 m, we often could not detect noise and light treatments, suggesting that birds may also have been unable to detect them. We excluded 21 trials from the statistical analysis because they contained no detections that met the inclusion criteria.

296 **Statistical analysis**

297 If birds advance the onset of song in response to noise or light, then that effect should be
298 most evident when birds first start to sing. For each trial, we identified the first five
299 vocalizations produced after midnight by each passerine species. The five vocalizations
300 were derived from the subset of 10 vocalizations that we originally annotated and that
301 met all of the inclusion criteria. Our rationale for including the first five vocalizations,
302 rather than the first vocalization only, was that birds sometimes produce isolated songs at
303 night that do not reflect the general onset of the individual's dawn chorus (Leopold and
304 Eynon 1961). For each of the five songs from each species, we noted the time it was
305 produced (number of minutes after midnight) and its 2-dimensional Euclidean distance
306 from the experimental disturbance. If the trial included a light and speaker that were
307 slightly separated, we calculated distances to the midpoint between them. For control
308 trials, distances were calculated relative to the center of the array. Time of production and
309 distance to disturbance for the first five vocalizations from each species were used as
310 dependent variables in subsequent statistical analyses.

311 We used linear mixed-effects models to test for the effects of noise (present versus
312 absent), light (present versus absent), and their two-way interaction on each dependent
313 variable. Noise and light treatments were included as categorical variables with fixed
314 effects, and array number and species identity as categorical variables with random
315 effects to control for non-independence among data derived from the same location and
316 species. We analyzed all passerines combined, and then conducted species-specific

317 analyses for the six most common species, as determined by the number of arrays in
318 which they were detected (Table 1). These included: boreal chickadee, dark-eyed junco,
319 ruby-crowned kinglet, Swainson's thrush, white-throated sparrow, and yellow-rumped
320 warbler. Analyses were conducted in R (R Core Team 2019) using the lme4 (Bates et al.
321 2015) and lmerTest (Kuznetsova et al. 2017) packages. Results were considered
322 statistically significant where $P \leq 0.05$.

323 We included five colors of light to ensure that our stimuli represented the broad
324 category of light disturbance, and to permit a preliminary investigation into the effects of
325 light color on avian responses. Previous research showed that birds respond differently to
326 different colors of light (Poot et al. 2008). It is therefore possible that responses to one
327 color could have offset responses to another in our analysis of treatment effects. For
328 example, birds might have been attracted to red lights, but repelled by green lights. We
329 therefore conducted additional analyses to determine if either of our two response
330 variables were influenced by light color. For the subset of 73 trials that did not involve a
331 noise playback, we compared each response variable from the passerine dataset among
332 the six light conditions using another linear mixed-effects model. Light colour was
333 included as a categorical variable with fixed effects, and array and species were included
334 as categorical variables with random effects. Note that sample sizes among treatment
335 groups were variable and, for some colors, quite small (no light N = 38 arrays, cool white N
336 = 8, warm white N = 6, red N = 9, green N = 7, blue N = 5). Results should therefore be
337 interpreted with caution.

RESULTS

Passerine analysis

When all species were analyzed together, the first five vocalizations from each species occurred at 0450 h ± 10 min (mean ± SE; determined from a linear mixed-effects model including intercept as a fixed effect and array identity and species as random effects; *N* = 887 songs from 89 arrays and 27 species; the model used minutes past midnight as the dependent variable, but this was converted to local time here). For reference, sunrise at the time and location of our study occurred at 0440 h ± 7.31 min (mean ± SD; range: 0433–0459 h; www.timeanddate.com). Although isolated songs were detected throughout the night (see also Leopold and Eynon 1961), none of the species analyzed are considered to be nocturnal or to sing regularly at night (La 2012). The time of the first five vocalizations was not affected by the presence or absence of experimental noise or light (Table 2).

The average distance to disturbance during the first five vocalizations was 18.4 ± 0.9 m (mean ± SE; determined from a linear mixed-effects model including intercept as a fixed effect and array identity and species as random effects; *N* = 887 songs from 89 arrays and 27 species; Figure 1). There was a statistically significant effect of treatment on distance, with birds being attracted to noise (Table 2; Figure 1). There was no effect of light or the interaction between noise and light (Table 2; Figure 1).

The color of light did not affect the time of the first five vocalizations or the

359 distance of the vocalizing bird to the disturbance (Table 3).

360 The results were robust in three important ways. First, the response variables were
361 not derived from a single species that vocalized earlier than all the rest, but, rather, from
362 the vocalizations of 23 different passerine species (Tables 1–2). Second, the effect of noise
363 on distance to disturbance was not driven by the very strong effect seen in Swainson's
364 Thrush (see below), since the results remained identical with respect to statistical
365 significance when Swainson's Thrush was removed from the passerine analysis. Third, the
366 findings were not affected by our choice of inclusion criteria (i.e., that vocalizations were
367 localized to within 30 m of the disturbance with a localization error of 0.02 or less). We re-
368 ran the analyses using all combinations of localization error (0.01, 0.02, 0.03, 0.05, 0.1, no
369 limit) and distance (20, 30, and 40 m) and the results with respect to statistical significance
370 remained similar (Supplementary Materials). Specifically, there was a statistically
371 significant attraction to noise in 17 of the 18 models; the only exception was when
372 distance was set to 40 m and localization error to 'no limit.' For one of 18 combinations
373 (distance = 20 m x error = no limit), there was also a statistically significant interaction
374 between noise and light, such that the attractive effect of noise weakened in the presence
375 of light. Finally, for three combinations (distance = 40 m x error = 0.01, 0.05, 0.1), light
376 significantly repelled birds.

377

378 **Single-species analyses**

379 We conducted species-specific analyses on the six most common species (boreal

chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, white-throated sparrow, yellow-rumped warbler), though we note that sample sizes were smaller than for the passerine analysis (Table 2). We did not apply any adjustments to experimentwise error because the analysis and conclusions for one species are independent of those for another species.

The time of the first five vocalizations was not affected by noise, light, or the interaction between noise and light for five of the six species, including boreal chickadee, dark-eyed junco, ruby-crowned kinglet, Swainson's thrush, and white-throated sparrow (Table 2). The only exception was yellow-rumped warbler, which began vocalizing earlier when noise was present versus absent (Table 2; Figure 2). The average distance to disturbance was also not affected by the experimental manipulations for five of the six species, including boreal chickadee, dark-eyed junco, ruby-crowned kinglet, white-throated sparrow, and yellow-rumped warbler (Table 2). For Swainson's thrush, however, there was a statistically significant effect of the disturbance treatments, with individuals being attracted to noise and repelled by light (Table 2; Figure 3). There was also a significant interaction between noise and light for Swainson's thrush, with individuals being attracted to the combination of light and noise (Table 2; Figure 3). Finally, although many of the analyses were not statistically significant, it is worth noting that, for all six species, birds were, on average, closer to the disturbance when noise was present versus absent (Table 2), which is unlikely to have occurred by chance (binomial test: $P = 0.031$).

401 **DISCUSSION**

402 We manipulated the presence of anthropogenic noise and light to determine their
403 independent and combined effects on the vocal and spatial behavior of wild birds. When
404 all passerine species were analyzed together, none of the treatments influenced when
405 birds began vocalizing. However, contrary to our predictions, birds were attracted to
406 anthropogenic noise and, depending on the localization settings used, either repelled by
407 or not attracted to anthropogenic light. We found no evidence that birds responded
408 differently to different colours of light. The within-species analyses of six common boreal
409 bird species revealed similar patterns to the passerine analysis, though most of the effects
410 were not statistically significant. There were two exceptions. Swainson's thrush was
411 attracted to noise and the combination of noise and light, and was repelled by light when
412 presented in the absence of noise. Yellow-rumped warbler also began singing earlier in
413 the presence of noise.

414 Traffic noise attracted passerines over spatial scales of 20 to 40 m (Table 2; Figures
415 1, 3; Supplemental Materials), which contradicts our prediction and previous studies.
416 Bayne et al. (2008) found that passerine density in the breeding season was lower in areas
417 adjacent to noise-generating compressor stations than in control areas adjacent to quiet,
418 but otherwise similar, oil well pads. Similarly, Blickley et al. (2012) found fewer male
419 Greater Sage-Grouse (*Centrocercus urophasianus*) at leks paired with experimental traffic
420 noise than at silent control leks. Finally, bird densities during the migratory and breeding
421 seasons were lower near real (Reijnen et al. 1995) and simulated (McClure et al. 2016)

422 roads than at sites away from roads. A possible explanation for our discordant result is
423 that these other studies measured avian densities next to chronic noise that began before
424 birds arrived on the breeding grounds. The density of birds at those sites was likely
425 governed by whether newly arriving migrants (Bayne et al. 2008; McClure et al. 2016) or
426 males establishing leks (Blickley et al. 2012) chose to settle near noisy sites. In contrast,
427 we measured the proximity of breeding birds to a noise source that was introduced into
428 their established breeding territories. It is therefore possible that birds avoid noisy sites
429 when choosing where to settle, but approach noise when it occurs within or near their
430 established territories. An alternative explanation is that birds approach novel noise
431 stimuli because they are curious, and then avoid those stimuli after chronic exposure. This
432 seems unlikely because our stimuli typically played for 11.5 hours before birds began
433 singing, though it is possible that avoidance occurs only after days or weeks of exposure.
434 Noise did not affect when birds began singing, as we had hypothesized. Previous
435 studies examining the effects of traffic noise on the timing of the dawn chorus involved
436 natural traffic noise that fluctuated throughout the day (e.g., rush hour). The relatively
437 quiet periods between times of heavy traffic may have provided birds in those studies
438 with predictable periods of relief from acoustic masking, which may have prompted them
439 to shift song production to those times (Fuller et al. 2007; Cartwright et al. 2014). In our
440 study, the simulated traffic occurred at a constant rate throughout the relatively short
441 playback period (1700 h until 0800 h the following day), thereby providing no predictable
442 cues about when the noise might subside. We also had three different noise stimuli to

443 minimize potential effects of pseudoreplication. All stimuli were of traffic noise, but they
444 included different rates of passing vehicles. It is possible that some species tolerate low
445 levels of noise, and that the onset of singing changes only in response to louder noise or
446 higher rates of traffic. For example, some species may adapt to road noise associated with
447 small, rural road traffic, but not to the constant and intense traffic noise associated with
448 major urban freeways (Reijen et al. 1995). Another possibility is that these previous
449 studies were correlational in nature, and that the reduction in song production during
450 peak traffic times was caused by increased exhaust or light from headlights, rather than by
451 the associated increase in noise (Summers et al. 2011). Additional experimental research
452 is needed to disentangle the effects of noise from the other forms of disturbance that
453 commonly co-occur with noise (e.g., roadways, urban development, vehicles, and
454 exhaust), particularly since the effects of noise on the timing of bird song have been
455 inconsistent in the literature (Ortega 2012; Dominoni et al. 2016).

456 Vocalizing passerines were not attracted to artificial light when the different colors
457 of light were combined into a single treatment (Figure 1). Depending on the localization
458 settings used, birds may even have been repelled by light. This was surprising because
459 several studies show that birds are attracted to bright lights (Longcore and Rich 2004;
460 Montevecchi 2006; van Doren et al. 2017). However, most of those studies involved birds
461 that were flying during migration or long-distance foraging excursions (Ronconi et al.
462 2015; van Doren et al. 2017; McLaren et al. 2018). In contrast, our study involved
463 passerines in established breeding territories, suggesting that attraction to light occurs

464 primarily during long-distance flight. Another possibility is that, compared to the lights
465 used in our study, those used in most previous studies were more visible because they
466 were more powerful and were located in open areas (e.g., oil platforms in the open ocean,
467 light projected skyward, urban glow found above cities; Ronconi et al. 2015; van Doren et
468 al. 2017; McLaren et al. 2018). The lights used in our study were less powerful and were
469 located below the canopy of a dense forest, which likely reduced the light's visibility to
470 birds singing from within the canopy.

471 Artificial lighting did not cause passerine birds to sing earlier, which contrasts with
472 previous studies (Kempenaers et al. 2010; Dominoni et al. 2013). However, those studies
473 compared birds in brightly lit cities to those living in rural areas with few or no lights. In
474 contrast, our study compared birds' responses to a single dim light versus no light. The
475 intensity of our light treatment was therefore much weaker than in previous studies.
476 Interestingly, Da Silva et al. (2017) also used low-intensity lighting and also failed to detect
477 an effect of light on the onset of dawn song. Together, these studies suggest that the
478 brightness, not just the presence, of artificial lighting may be important in stimulating
479 birds to sing prematurely. This is consistent with Thomas et al. (2002), which showed that
480 species with larger eyes that are more sensitive to dim light begin singing earlier in the
481 morning.

482 Our species-specific analyses revealed similarities and differences to our overall
483 passerine analysis. First, the species-level analyses supported the finding that passerines
484 are generally attracted to traffic noise. Although the analyses of individual species were

485 generally non-significant, birds from all six species were closer, on average, to the noise
486 stimulus than to the silent control, which is unlikely to have occurred by chance. Second,
487 Swainson's thrush was attracted to noise and repelled by light. Passerines were also
488 attracted to noise and, depending on the localization settings, repelled by light, but the
489 effects were much stronger in Swainson's thrush. Of the six species analyzed, Swainson's
490 thrush is the only one classified as an interior forest specialist (Whitaker and Montevecchi
491 1999). The other five species are categorized as 'forest generalists' (boreal chickadee and
492 ruby-crowned kinglet), 'open-edge species' (dark-eyed junco, white-throated sparrow), or
493 'ubiquitous species' (yellow-rumped warbler), which all include or tolerate anthropogenic
494 edge habitat in their breeding range. Therefore, habitat specialization and avoidance of
495 disturbed habitat may make Swainson's thrush more sensitive and responsive to noise and
496 light disturbances that occur suddenly within their breeding territories (Bonier et al.
497 2007). Another possibility is that, because Swainson's thrush forages on the ground
498 (Holmes and Robinson 1988), it may have been more exposed than the canopy-dwelling
499 species to the light and noise stimuli. Third, unlike passerines in general, yellow-rumped
500 warblers sang earlier when noise was present. Yellow-rumped warblers are one of the first
501 warbler species to begin singing in the morning (Morse 1989). It is possible that the forest
502 was quieter, and the traffic noise more obvious, when they began singing, as compared to
503 when most species began singing.

504 Our approach provided experimental control and passive monitoring of 31 species
505 in a natural context, but it also had several limitations. First, microphone arrays only

506 detect and localize vocalizing animals, which means it is possible that we missed non-vocal
507 responses to experimental treatments. This could not account for the observed attraction
508 to noise, but could explain the unexpected finding that birds were not attracted to light.
509 For example, some birds might have approached the light stimulus in silence, while others
510 remained distant and singing. A second limitation is that our microphone arrays could only
511 detect and localize birds within 40 m of the disturbance treatments. It is possible that
512 some spatial and vocal responses to experimental treatments occurred beyond this
513 distance, particularly for species with large territories, and that these responses were
514 therefore excluded from our analyses. A third limitation is that our playback equipment
515 needed to be portable, which limited the intensity of our noise and light stimuli. However,
516 all noise and light attenuate with increasing distance from their source, thereby forming
517 intensity gradients. Although our stimuli did not replicate the maximum intensities of light
518 and noise that might be found sporadically in the environment, they undoubtedly
519 simulated intensities experienced by many free-living animals, including those living close
520 to low-intensity disturbances and those living far away from high-intensity disturbances.
521 Multiple forms of disturbance often co-occur, making it difficult for managers to
522 know which disturbances affect animals and should be mitigated. We found that passerine
523 birds are attracted to traffic noise, but not to light, which often accompanies traffic noise
524 (e.g., streetlights, vehicle headlights). If birds are drawn to traffic noise, then they may
525 experience an increased likelihood of fatal collision with vehicles at roadsides (Kociolek et
526 al. 2011). Although anecdotal, we observed many dead passerines that had been struck by

vehicles along the roadways connecting our study sites. Another concern is that attraction to traffic noise may cause birds to reside near roadsides that negatively affect their reproductive success (Halfwerk et al. 2011b) or increase their predation risk (Meillere et al. 2015; Templeton et al. 2016) through the masking of acoustic signals. Being attracted to traffic noise could also increase exposure to air pollution from vehicle exhaust or the risk of poisoning through the consumption of de-icing agents (Kociolek et al. 2011). Our study suggests that conservation biologists and land managers should consider the effects of noise on birds, as well as the use of noise mitigation technologies that reduce noise in vulnerable or ecologically important habitat. Furthermore, given that our trials were conducted in undisturbed areas within the forest, an important future direction would be to repeat our study in disturbed areas to determine whether chronic exposure to noise and light pollution alters the behavioural responses to additional noise observed in the current study.

In conclusion, our study is the first to our knowledge to use microphone arrays to test the independent and combined effects of anthropogenic light and noise on the singing and spatial behavior of wild birds. This promising technology allowed us to passively and accurately quantify the responses of 31 species over a prolonged period of time (8 hours per trial) across a broad geographic area (110 sites with blanket coverage over a 30-m radius at each site, or approximately 31 ha). Our results show that birds in the boreal forest are attracted to traffic noise, but not to artificial lighting.

SUPPLEMENTAL MATERIAL

Supplementary materials are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Hennigar et al. (2019).

Declarations of conflict of interest: none

568 **Ethical note:** All research complied with the 'Guidelines for the treatment of animals in
569 behavioural research and teaching' set forth by the Animal Behavior Society and the
570 Association for the Study of Animal Behavior, and was approved under Memorial
571 University of Newfoundland animal use protocol number 15-02-DW.
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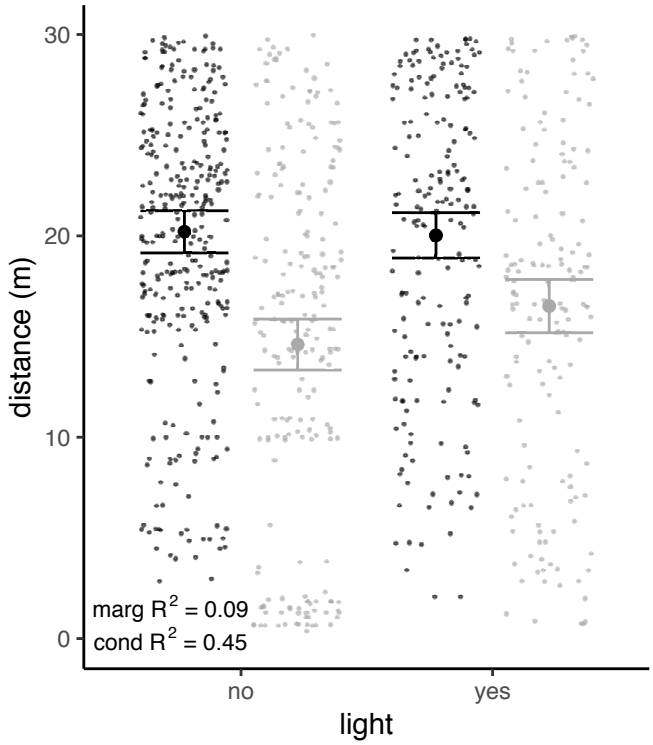

713

714 **Figure 1** The effects of noise (noise absent = black; noise present = gray), light, and the
715 interaction between noise and light on the distance to disturbance (or distance to the
716 center of the array for control trials) of the first five vocalizations produced by each
717 species during each trial (*N* = 887 songs from 27 species and 89 trials). Large dots and
718 error bars show mean ± SE, as calculated from a linear mixed-effects model including
719 noise (present vs. absent), light (present vs. absent), and the two-way interaction between
720 noise and light as fixed effects, and array identity and species as random effects (see text
721 for details of models).Marginal R^2 (i.e., variance explained by fixed factors) and conditional
722 R^2 (i.e., variance explained by fixed and random factors) are calculated according to
723 Nakagawa and Schielzeth (2013) and shown in the lower left of the plot.

724

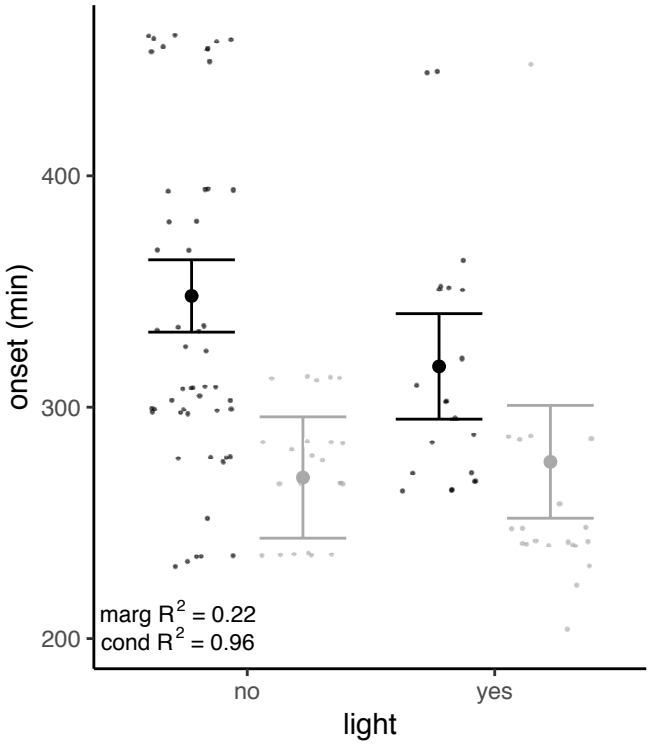

Figure 2 The effects of noise (noise absent = black; noise present = gray), light, and the interaction between noise and light on the time (number of minutes past midnight) of the first five vocalizations produced by yellow-rumped warblers (*N* = 115 songs from 38 trials). Large dots and error bars show the mean ± SE, as calculated from a linear mixed-effects model including noise (present vs. absent), light (present vs. absent), and the two-way interaction between noise and light as fixed effects, and array identity as a random effect (see text for details of models). Marginal R^2 (i.e., variance explained by fixed factors) and conditional R^2 (i.e., variance explained by fixed and random factors) are calculated according to Nakagawa and Schielzeth (2013) and shown in the lower left of the plot.

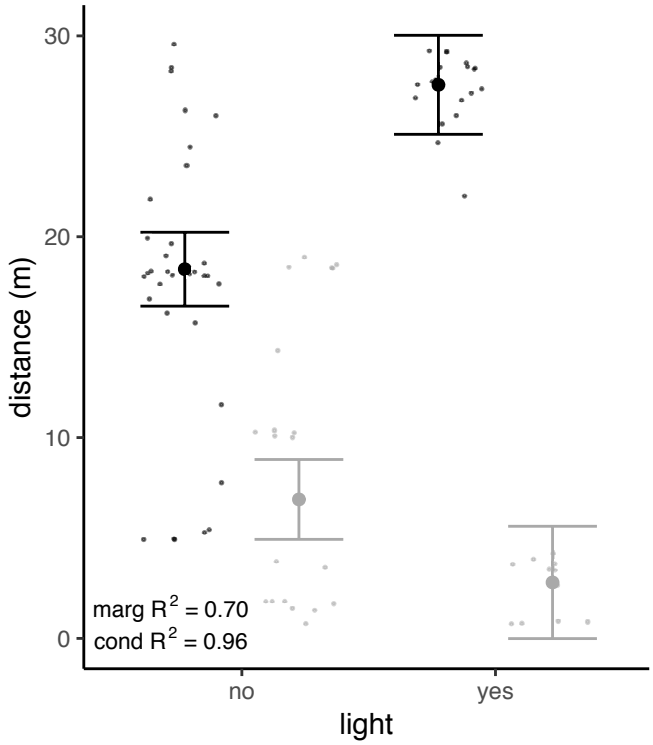

Figure 3 The effects of noise (noise absent = black; noise present = gray), light, and the interaction between noise and light on the distance to disturbance (or distance to the center of the array for control trials) of the first five vocalizations produced by Swainson's thrush during each trial (*N* = 83 songs from 26 trials). Large dots and error bars show the mean ± SE, as calculated from a linear mixed-effects model including noise (present vs. absent), light (present vs. absent), and the two-way interaction between noise and light as fixed effects, and array identity as a random effect (see text for details of models). Marginal R^2 (i.e., variance explained by fixed factors) and conditional R^2 (i.e., variance explained by fixed and random factors) are calculated according to Nakagawa and Schielzeth (2013) and shown in the lower left of the plot.

Table 1 Avian vocalizations included in this study.

Common name	Scientific name	Vocalizations detected	Vocalizations analyzed	Bandpass filter (Hz)
alder flycatcher	*Empidonax alnorum*	10 (82)	2 (6)	2387–6594
American redstart	*Setophaga ruticilla*	1 (7)	0 (0)	3729–9013
American robin	*Turdus migratorius*	55 (490)	13 (31)	1760–4969
black-throated green warbler	*Setophaga virens*	37 (296)	12 (29)	3042–6470
blackpoll warbler	*Setophaga striata*	1 (10)	1 (1)	4008–9223
boreal chickadee	***Poecile hudsonicus***	**58 (455)**	**20 (64)**	**3348–8336**
brown creeper	*Certhia americana*	8 (49)	2 (3)	3878–7309
Cape May warbler	*Setophaga tigrina*	15 (122)	2 (6)	3545–9291
common raven	*Corvus corax*	7 (52)	1 (1)	931–1875
common redpoll	*Acanthis flammea*	6 (39)	3 (4)	2830–6650
Connecticut warbler	*Oporornis agilis*	1 (10)	0 (0)	3090–6040
dark-eyed junco	***Junco hyemalis***	**88 (816)**	**36 (139)**	**2975–6839**

764	fox sparrow	*Passerella iliaca*	78	(713)	16	(41)	2134–5774
765	golden-crowned kinglet	*Regulus satrapa*	1	(1)	0	(0)	6840–8250
766	hermit thrush	*Catharus guttatus*	47	(427)	7	(12)	2347–5308
767	Lincoln's sparrow	*Melospiza lincolnii*	29	(198)	15	(43)	1557–7204
768	magnolia warbler	*Setophaga magnolia*	9	(77)	4	(10)	2460–8032
769	northern waterthrush	*Parkesia noveboracensis*	15	(110)	4	(18)	2196–7672
770	orange-crowned warbler	*Oreothlypis celata*	28	(222)	11	(26)	2451–8544
771	palm warbler	*Setophaga palmarum*	1	(10)	1	(4)	4500–8000
772	Philadelphia warbler	*Vireo philadelphicus*	2	(13)	0	(0)	1600–6200
773	pine grosbeak	*Pinicola enucleator*	30	(225)	8	(20)	2085–5223
774	pine siskin	*Spinus pinus*	38	(311)	15	(37)	3665–6875
775	red-breasted nuthatch	*Sitta canadensis*	15	(92)	5	(10)	1046–6844
776	**ruby-crowned kinglet**	***Regulus calendula***	**79**	**(713)**	**31**	**(96)**	**1982–6518**
777	**Swainson's thrush**	***Catharus ustulatus***	**71**	**(702)**	**26**	**(83)**	**1630–5503**
778	Tennessee warbler	*Oreothlypis peregrina*	22	(214)	10	(32)	2533–9993

white-throated sparrow	***Zonotrichia albicollis***	**80 (702)**	**20 (43)**	**2235–7130**
winter wren	*Troglodytes hiemalis*	7 (62)	3 (8)	2579–9491
yellow-bellied flycatcher	*Empidonax flaviventris*	2 (20)	1 (5)	2761–5994
yellow-rumped warbler	***Setophaga coronata***	**79 (667)**	**38 (115)**	**2827–6520**

"Vocalizations detected" shows the number of arrays in which a species was detected, and, in parentheses, the number of vocalizations detected from that species across all arrays. Vocalizations were considered 'detected' if they were visible on the spectrograms corresponding to three of the four corners of the array. For our study, we annotated a maximum of 10 vocalizations per species per array. "Vocalizations analyzed" shows the same information, but based on the subset of vocalizations that were localized to within 30 m of the experimental disturbance (or of the center of the array for control trials) with a localization error of 0.02 or less (see text for explanation of this error term). We retained for our analysis a maximum of the first five vocalizations per species per array that met these inclusion criteria. The six species that were present in the greatest number of arrays, as defined by the column ‘Vocalizations analyzed’, were also analyzed individually and are shown in bold.

Table 2. Effects of light and noise on song production.

	Time of onset			Distance to disturbance		
Model	coefficient (± SE)	*t*	*P*	coefficient (± SE)	*t*	*P*
all passerines (*N* = 887 songs from 89 arrays and 27 species)						
Intercept	**288.1 ± 12.5**	**23.1**	**< 0.001**	**20.2 ± 1.0**	**19.3**	**< 0.001**
Noise	7.3 ± 15.7	0.5	0.641	-5.6 ± 1.3	-4.2	**< 0.001**
Light	6.9 ± 13.7	0.5	0.618	-0.2 ± 1.2	-0.1	0.882
Noise x light	-25.6 ± 22.8	-1.1	0.266	2.1 ± 2.0	1.1	0.289
boreal chickadee (*N* = 64 songs from 20 arrays)						
Intercept	**304.1 ± 23.1**	**13.2**	**< 0.001**	**19.5 ± 2.3**	**8.5**	**< 0.001**
Noise	73.2 ± 46.1	1.6	0.132	-1.0 ± 4.7	-0.2	0.831
Light	12.1 ± 46.1	0.3	0.796	0.8 ± 4.6	0.2	0.855
Noise x light	-85.5 ± 68.4	-1.3	0.229	-2.7 ± 6.8	-0.4	0.694
dark-eyed junco (*N* = 139 songs from 36 arrays)						
Intercept	**260.2 ± 13.3**	**19.6**	**< 0.001**	**21.9 ± 1.7**	**13.0**	**< 0.001**
Noise	-11.1 ± 23.7	-0.5	0.642	-2.9 ± 3.0	-1.0	0.335
Light	26.6 ± 21.0	1.3	0.215	-4.2 ± 2.7	-1.6	0.126
Noise x light	10.0 ± 38.5	0.3	0.797	-1.6 ± 4.9	-0.3	0.741
ruby-crowned kinglet (*N* = 96 songs from 31 arrays)						
Intercept	**307.7 ± 21.1**	**14.6**	**< 0.001**	**19.3 ± 1.9**	**10.0**	**< 0.001**
Noise	-9.5 ± 34.7	-0.3	0.786	-3.8 ± 3.1	-1.2	0.235

Light	1.9 ± 36.4	0.1	0.958	3.1 ± 3.3	0.9	0.357
Noise x light	5.8 ± 54.4	0.1	0.916	0.4 ± 4.8	0.1	0.926
Swainson's thrush (*N* = 83 songs from 26 arrays)						
Intercept	**223.5 ± 6.0**	**37.1**	**< 0.001**	**18.4 ± 1.8**	**10.0**	**< 0.001**
Noise	-5.9 ± 8.8	-0.7	0.506	**-11.5 ± 2.7**	**-4.2**	**< 0.001**
Light	15.5 ± 10.1	1.5	0.139	**9.2 ± 3.1**	**3.0**	**0.007**
Noise x light	-23.0 ± 15.0	-1.5	0.138	**-13.3 ± 4.6**	**-2.9**	**0.008**
white-throated sparrow (*N* = 43 songs from 20 arrays)						
Intercept	**264.2 ± 24.1**	**11.0**	**< 0.001**	**20.8 ± 3.0**	**6.8**	**< 0.001**
Noise	-55.0 ± 50.6	-1.1	0.292	-12.6 ± 6.4	-2.0	0.068
Light	-70.4 ± 35.3	-2.0	0.062	-4.3 ± 4.5	-1.0	0.355
Noise x light	68.5 ± 62.8	1.1	0.291	9.0 ± 8.0	1.1	0.278
yellow-rumped warbler (*N* = 115 songs from 38 arrays)						
Intercept	**348.1 ± 15.6**	**22.3**	**< 0.001**	**21.4 ± 1.2**	**17.7**	**< 0.001**
Noise	**-78.5 ± 30.5**	**-2.6**	**0.015**	-1.8 ± 2.3	-0.8	0.448
Light	-30.4 ± 27.6	-1.1	0.279	2.0 ± 2.2	0.9	0.358
Noise x light	37.2 ± 45.2	0.8	0.416	0.5 ± 3.5	0.1	0.888

Analyses were conducted on all passerine species combined, and separately on the six most common species, as determined by the number of arrays in which they were present. Response variables include the time when each song was produced (minutes past midnight) and the distance between the singer and disturbance during song production

834 for the first five songs per species per array. Responses were modeled using linear mixed-
835 effects models (restricted maximum likelihood) with array identity as a random effect.
836 Estimates for each factor are for the level of the factor where the treatment (noise, light)
837 is present, and *t*-tests are conducted using Satterthwaite's method. SE = standard error.
838 Statistically significant effects ($\propto = 0.05$) are in bold.
839 Random effects for time of song production models (variance $\pm$ standard deviation):
840 all passerines: array = 2287 $\pm$ 48; species = 1685 $\pm$ 41; residual = 2163 $\pm$ 47;
841 boreal chickadee: array = 4746 $\pm$ 69; residual = 82 $\pm$ 9;
842 dark-eyed junco: array = 2587 $\pm$ 51; residual = 198 $\pm$ 14;
843 ruby-crowned kinglet: array = 5157 $\pm$ 72; residual = 295 $\pm$ 17;
844 Swainson's thrush: array = 326 $\pm$ 18; residual = 0 $\pm$ 1;
845 white-throated sparrow: array = 3054 $\pm$ 55; residual = 1434 $\pm$ 38;
846 yellow-rumped warbler: array = 4046 $\pm$ 64; residual = 205 $\pm$ 14;
847 Random effects for distance to disturbance models (variance $\pm$ standard deviation):
848 all passerines: array = 13.9 $\pm$ 3.7; species = 10.5 $\pm$ 3.2; residual = 36.6 $\pm$ 6.1;
849 boreal chickadee: array = 43.3 $\pm$ 6.6; residual = 10.5 $\pm$ 3.2;
850 dark-eyed junco: array = 40.4 $\pm$ 6.4; residual = 6.2 $\pm$ 2.5;
851 ruby-crowned kinglet: array = 30.8 $\pm$ 5.6; residual = 25.8 $\pm$ 5.1;
852 Swainson's thrush: array = 28.8 $\pm$ 5.4; residual = 4.1 $\pm$ 2.0;
853 white-throated sparrow: array = 55.3 $\pm$ 7.4; residual = 13.5 $\pm$ 3.7;
854 yellow-rumped warbler: array = 18.2 $\pm$ 4.3; residual = 14.2 $\pm$ 3.8;
855

Table 3 Effects of light color on song production in passerines

Response	Effect	Estimate ± SE	*t*	*P*
[a]Time	Intercept	281.1 ± 13.6	20.7	<0.001
	Colour (blue)	-36.6 ± 28.1	-1.3	0.198
	Colour (cool white)	-0.5 ± 22.0	0.0	0.981
	Colour (green)	2.0 ± 23.6	0.1	0.933
	Colour (red)	37.6 ± 23.4	1.6	0.115
	Colour (warm white)	42.7 ± 30.8	1.4	0.174
[b]Distance	Intercept	19.8 ± 0.9	21.5	<0.001
	Colour (blue)	-4.6 ± 2.4	-1.9	0.060
	Colour (cool white)	3.7 ± 1.9	2.0	0.055
	Colour (green)	0.3 ± 2.0	0.1	0.885
	Colour (red)	1.4 ± 2.0	0.7	0.486
	Colour (warm white)	-4.1 ± 2.6	-1.6	0.119

Response variables include the time when each song was produced (minutes past midnight) and the distance between the singer and disturbance during song production for the first five songs of each species. Responses were modeled using linear mixed-effects models (restricted maximum likelihood) with array identity and species as random effects. Estimates are reported for the level of the factor shown in parentheses, relative to the no light condition, and *t*-tests are conducted using Satterthwaite's method. Only arrays in

877 which the noise treatment was absent were included. *N* = 514 songs from 57 arrays and

878 24 species. SE = standard error.

879 [a]Random effects (variance ± standard deviation): array (2357 ± 49); species (2107 ± 46);

880 residual (1942 ± 44)

881 [b]Random effects (variance ± standard deviation): array (15 ± 4); species (4 ± 2); residual

882 (30 ± 5)

883

Table S1. Effects of sampling area radius and localization error on statistical analyses.

Model	Time of onset		Distance to disturbance	
	t	*P*	*t*	*P*
Sampling area radius = 20 m; localization error ≤ 0.01				
N = 415 songs from 64 arrays and 23 species				
Intercept	**15.8**	**<0.001**	**13.7**	**< 0.001**
Noise	0.4	0.658	**-2.8**	**0.008**
Light	0.3	0.793	-1.2	0.221
Noise x light	-0.8	0.414	1.9	0.068
Sampling area radius = 20 m; localization error ≤ 0.02				
N = 529 songs from 74 arrays and 26 species				
Intercept	**18.0**	**< 0.001**	**15.0**	**< 0.001**
Noise	0.7	0.463	**-3.3**	**< 0.002**
Light	0.1	0.923	-1.4	0.180
Noise x light	-1.1	0.270	1.9	0.056
Sampling area radius = 20 m; localization error ≤ 0.03				
N = 585 songs from 78 arrays and 27 species				
Intercept	**19.4**	**< 0.001**	**16.0**	**< 0.001**
Noise	0.5	0.585	**-3.8**	**< 0.001**
Light	-0.3	0.790	-1.3	0.207
Noise x light	-1.0	0.346	2.0	0.053
Sampling area radius = 20 m; localization error ≤ 0.05				
N = 672 songs from 84 arrays and 27 species				
Intercept	**21.2**	**< 0.001**	**17.1**	**< 0.001**
Noise	0.9	0.361	**-3.8**	**< 0.001**
Light	0.1	0.882	-1.0	0.335
Noise x light	-1.5	0.127	1.7	0.100
Sampling area radius = 20 m; localization error ≤ 0.1				
N = 808 songs from 93 arrays and 27 species				
Intercept	**24.1**	**< 0.001**	**19.2**	**< 0.001**
Noise	0.3	0.802	**-3.4**	**0.001**
Light	-0.1	0.896	-0.7	0.505
Noise x light	-1.2	0.221	1.2	0.229
Sampling area radius = 20 m; localization error = no limit				
N = 1264 songs from 102 arrays and 27 species				
Intercept	**27.3**	**< 0.001**	**25.1**	**< 0.001**
Noise	0.0	0.967	**-3.4**	**< 0.001**
Light	0.0	0.975	-0.7	0.497
Noise x light	-1.1	0.274	**2.0**	**0.049**

Sampling area radius = 30 m; localization error ≤ 0.01

N = 653 songs from 80 arrays and 26 species

Intercept	**21.2**	**< 0.001**	**16.6**	**< 0.001**
Noise	0.5	0.638	**-3.6**	**< 0.001**
Light	0.7	0.512	0.1	0.907
Noise x light	-1.4	0.154	1.2	0.222

Sampling area radius = 30 m; localization error ≤ 0.03

N = 998 songs from 94 arrays and 27 species

Intercept	**24.9**	**< 0.001**	**20.6**	**< 0.001**
Noise	0.2	0.822	**-4.3**	**< 0.001**
Light	0.6	0.529	0.2	0.846
Noise x light	-1.3	0.204	1.0	0.309

Sampling area radius = 30 m; localization error ≤ 0.05

N = 1169 songs from 100 arrays and 28 species

Intercept	**27.4**	**< 0.001**	**21.8**	**< 0.001**
Noise	-0.2	0.833	**-3.9**	**< 0.001**
Night	0.4	0.728	0.5	0.647
Noise x light	-1.1	0.263	0.5	0.650

Sampling area radius = 30 m; localization error ≤ 0.1

N = 1497 songs from 103 arrays and 29 species

Intercept	**27.8**	**< 0.001**	**24.6**	**< 0.001**
Noise	-0.3	0.780	**-3.7**	**< 0.001**
Light	0.3	0.743	-0.2	0.879
Noise x light	-1.3	0.203	0.2	0.848

Sampling area radius = 30 m; localization error = no limit

N = 2591 songs from 107 arrays and 30 species

Intercept	**27.2**	**< 0.001**	**35.6**	**< 0.001**
Noise	-0.9	0.368	**-3.5**	**< 0.001**
Light	0.9	0.361	-1.1	0.296
Noise x light	-0.8	0.404	1.1	0.275

Sampling area radius = 40 m; localization error ≤ 0.01

N = 856 songs from 89 arrays and 27 species

Intercept	**21.9**	**< 0.001**	**16.1**	**< 0.001**
Noise	0.6	0.553	**-3.2**	**0.002**
Light	0.0	0.993	**2.1**	**0.038**
Noise x light	-1.0	0.311	0.493	0.624

Sampling area radius = 40 m; localization error ≤ 0.02

N = 1174 songs from 100 arrays and 28 species

Intercept	**24.0**	**< 0.001**	**18.3**	**< 0.001**
Noise	0.7	0.514	**-3.5**	**< 0.001**
Light	-0.1	0.945	1.8	0.078
Noise x light	-0.7	0.457	0.8	0.444

Sampling area radius = 40 m; localization error ≤ 0.03

N = 1343 songs from 101 arrays and 28 species

Intercept	**25.2**	**< 0.001**	**19.6**	**< 0.001**
Noise	0.2	0.860	**-3.2**	**0.002**
Light	0.0	0.976	1.9	0.065
Noise x light	-0.6	0.549	0.3	0.772

Sampling area radius = 40 m; localization error ≤ 0.05

N = 1563 songs from 104 arrays and 28 species

Intercept	**26.7**	**< 0.001**	**22.0**	**< 0.001**
Noise	-0.3	0.783	**-2.8**	**0.006**
Light	0.0	0.964	**2.1**	**0.041**
Noise x light	-0.4	0.692	-0.2	0.869

Sampling area radius = 40 m; localization error ≤ 0.1

N = 1982 songs from 105 arrays and 29 species

Intercept	**27.3**	**< 0.001**	**24.5**	**< 0.001**
Noise	-0.3	0.793	**-2.3**	**0.024**
Light	-0.3	0.761	**2.0**	**0.046**
Noise x light	-0.4	0.702	-0.3	0.736

Sampling area radius = 40 m; localization error = no limit

N = 3147 songs from 107 arrays and 31 species

Intercept	**26.9**	**< 0.001**	**34.2**	**< 0.001**
Noise	-0.4	0.695	-1.6	0.110
Light	0.8	0.410	1.8	0.074
Noise x light	-0.7	0.460	-0.4	0.686

Sampling area radius is the distance from disturbance (or from the center of the array in control trials) over which vocalizations were considered for inclusion in the analysis. Localization error is a unitless measure of model fit derived from the localization procedure. For each combination of sampling area radius (20, 30, 40 m) and localization error (0.01, 0.02, 0.03, 0.05, 0.1, no limit), a linear mixed-effects model tested for the fixed effects of noise, light, and the interaction between noise and light on the time of onset and the distance to disturbance of the first five vocalizations produced by each passerine species. Array identity and species were included in each model as categorical variables with random effects. Statistically significant effects ($\propto$ = 0.05) effects are in bold. Note that results for sampling area radius = 30 m and localization error ≤ 0.02 are presented in the paper, so are not repeated here.